Biogeosciences Discuss., 4, 2007–2025, 2007
www.biogeosciences-discuss.net/4/2007/2007/

Biogeosciences Discussions is the access reviewed discussion forum of *Biogeosciences*

Temperature sensitivity of soil respiration is dependent on readily decomposable C substrate concentration

A. A. Larionova, I. V. Yevdokimov, and S. S. Bykhovets

Institute of Physicochemical and Biological Problems in Soil Science, RAS, 142290, Institutskaya 2, Pushchino, Moscow region, Russia

Received: 16 May 2007 – Accepted: 13 June 2007 – Published: 26 June 2007

Correspondence to: I. V. Yevdokimov (ilyaevd@rambler.ru)

Abstract

Temperature acclimation of soil organic matter (SOM) decomposition is one of the major uncertainties in predicting soil CO_2 efflux by the increase in global mean temperature. A reasonable explanation for an apparent acclimation proposed by Davidson and colleagues (2006) based on Michaelis-Menten kinetics suggests that temperature sensitivity decreases when both maximal activity of respiratory enzymes (V_{max}) and half- saturation constant (K_s) cancel each other upon temperature increase. We tested the hypothesis of the canceling effect by the mathematical simulation of the data obtained in the incubation experiments with forest and arable soils. Our data confirm the hypothesis and suggest that concentration of readily decomposable C substrate as glucose equivalent is an important factor controlling temperature sensitivity. The highest temperature sensitivity was observed when C substrate concentration was much lower than K_s. Increase of substrate content to the half-saturation constant resulted in temperature acclimation associated with the canceling effect. Addition of the substrate to the level providing respiration at a maximal rate V_{max} leads to the acclimation of the whole microbial community as such. However, growing microbial biomass was more sensitive to the temperature alterations. This study improves our understanding of the instability of temperature sensitivity of soil respiration under field conditions, explaining this phenomenon by changes in concentration of readily decomposable C substrate. It is worth noting that this pattern works regardless of the origin of C substrate: production by SOM decomposition, release into the soil by rhizodeposition, litter fall or drying-rewetting events.

1 Introduction

Variations in the temperature sensitivity of SOM decomposition are the main source of uncertainties in the models simulating C cycle. It has been suggested that temperature sensitivity of soil respiration is overestimated in global C cycle models (Thornley

and Cannell, 2001). Weak correlation between SOM decomposition and mean annual temperature (Giardina and Ryan, 2000), low temperature sensitivity of soil respiration in soil warming experiments with artificial soil heating (Jarvis and Linder, 2000; Melillo et al., 2002, Eliasson et al., 2005) confirmed the overestimation of respiration response to global warming. Recently Q_{10} value of 1.37 was determined by fitting a mechanistic decomposition model to a global data set of SOM (Ise and Moorcroft, 2006), assuming the importance of temperature acclimation of SOM decomposition.

Possible explanation for apparent acclimation based on Michaelis-Menten kinetics was proposed by Davidson et al. (2006). Microbial respiration is governed by enzyme kinetics and the activity of respiratory enzymes (R) as dependent on substrate concentration (C):

$$R = \frac{V_{\max} \times C}{K_m + C} \quad (1)$$

with maximal rate of enzyme activity $V_{\max}$ and half-saturation constant K_m. Both $V_{\max}$ and K_m increase with temperature resulting in the canceling effect. Thus, assuming the equal change of $V_{\max}$ and K_m, the response of R can be insensitive to temperature, although this suggestion was not confirmed in the experiments with soil microorganisms.

A modified Michaelis-Menten equation is used in soil studies mainly for determination of a readily decomposable C substrate as glucose equivalent (Sikora and McCoy, 1990; Bradley and Fyles, 1995; Badalucco and Hopkins, 1997), for partitioning of respiration activity of copiotrophic and oligotrophic components (Panikov et al., 1992), and for evaluation of predominant r-K strategy in microbial community (Blagodatsky et al., 1994). The parameters of Michaelis-Menten kinetics are determined from the experimentally measured relationships between the concentration of added glucose as respiration substrate and the short-term rate of soil CO_2 efflux. Glucose is widely used to determine the parameters of microbial growth and microbial biomass in soil since it is one of the main substances of the C substrate put into soil by rhizodeposition, as well as decomposition of cellulose and hemicellulose as the most abundant constituents of plant residues and microbial cell walls (Paul and Clark, 1996).

Sikora and McCoy (1992) modified Michaelis-Menten equation by adding a new parameter, AC, or a concentration of available carbon in soil. In some studies the proposed parameter is termed "content of native substrate", or S_n (Panikov et al., 1992; Blagodatsky et al., 1994). This parameter is equivalent to the added glucose concentration at zero CO_2 efflux, i.e. the negative substrate concentration when respiration is extrapolated to zero. Available carbon, or native substrate, turns over within several hours (Panikov et al., 1992), i.e. much faster than labile SOM pool fitted by single or double exponential decay function (Katterer et al., 1998; MacDonald et al., 1997), but both parameters reflect the activity of soil microorganisms decomposing SOM.

Our research was aimed to test the hypothesis of Davidson et al. (2006) using the modified Michaelis-Menten approach. To investigate the significance of the canceling effect, we performed 2 mo soil incubation at 12°C and 22°C. The parameters of glucose utilization were measured in soils taken from arable land depleted in SOM and forest site with high SOM content. In parallel, we monitored soil CO_2 efflux in the long term 12 mo incubation for determining rate constants of SOM decomposition by a double exponential decay equation.

2 Materials and methods

2.1 Site description and experimental design

We used soil (Luvic Phaeozem) collected from two sites, forest and arable, situated 4 km to the west of Pushchino, Moscow Region, Russia (54°50′ N, 37°35′ E).

The forest soil (0–20 cm; C_{org} 2.4%, pH 5.6) was sampled randomly in late October, 2005 in a secondary mixed aspen-lime-birch forest rich in herbs, with a mean tree age of 40–50 years. This site has been under forest for about 100 years. Soil samples from the arable site (0–20 cm; C_{org} 1.0%, pH 6.5) were collected in late September 2005 after winter wheat harvest from unfertilized plot of a field experiment (9 yr cereal rotation) established in the Field experimental station of the Institute of Physicochemical and

Biological Problems in Soil Science RAS.

Freshly sampled soil was sieved through 3 mm, with further removing fine roots with forceps. Then 50 g root-free soil samples were placed into 500 ml flasks and adjusted to 70% of water holding capacity (WHC). The soil samples were incubated with weekly addition of deionised water so as to keep wetness at a level of 70% WHC. One day after soil collection the flasks with the soil were placed in two chambers adjusted to the temperatures 12°C and 22°C, and incubated for over 2 months. After this incubation glucose solution was added to each sample to determine the kinetic parameters of the substrate utilization by soil microorganisms. In parallel the long term 12 mo incubation was performed for determining rate constants of SOM decomposition by a double exponential decay equation. To avoid the inhibition of soil respiration by high concentrations of CO_2 respired, headspace CO_2 concentrations were kept below 1.5%. CO_2 concentrations were determined 2–3 times a week during the first month of the incubation. At the advanced stages of the decomposition the interval was increased to 1–2 weeks. The flasks were ventilated for 30 min after each gas sampling.

2.2 Determination of kinetic parameters

Cumulative microbial respiration curves were fit to a double exponential decay model:

$$Y = 1 - A_0 e^{-k_1 t} - (1 - A_o) e^{-k_2 t} \quad (2)$$

where Y is the cumulative amount of C-CO_2 at time t expressed as a portion of organic C in soil, A_0 is a portion of labile pool, k_1 and k_2 are rate constants for labile and stable pools of organic matter, respectively.

Determination of the microbial growth rate involves simulation of the transition process of soil microorganisms from sustaining to the growing state, i.e. lag phase, as well as exponential phase of microbial growth after addition of the excess quantities of readily decomposable C substrate (Panikov and Sizova, 1996; Blagodatsky et al., 2000):

$$v(t) = v_u + v_c \times e^{\mu_{\max} t} \quad (3)$$

where v(t) is CO_2 production rate, t is time, $v_c$is the coupled respiration rate, v_u is the uncoupled respiration rate, and μ_{max} is the maximal specific growth rate when the microbial growth is unlimited.

CO_2 production by the soil amended with glucose at the rate of 4 mg Cg^{-1} dry soil was determined in the soil samples incubated at 22°C and 12°C. Gas probes were sampled periodically, after 30 min incubation of the soil samples with tightly sealed lids. After gas sampling the flasks with soil were ventilated till the next gas sampling.

Respiration response of the soil samples to the addition of increasing concentrations of C- substrate (glucose, at the rates of 10–1000 μg Cg^{-1} dry soil) was measured within 30 min after the substrate addition and simulated by the modified Michaelis-Menten kinetics (Sikora and McCoy, 1990; Panikov et al., 1992; Bradley and Fyles, 1996):

$$v = \frac{V_{max} \times (S + S_n)}{K_s + S + S_n} \quad (4)$$

where V_{max} is the maximal initial rate of respiration of soil microbial community, v is the initial rate of respiration of soil microbial community, K_S is the half-saturation constant (also known as Michaelis constant or affinity factor), S_n is the concentration of native (endogenous) available C substrate in soil, and S is the initial concentration of C substrate added to soil at the beginning of determination.

Glucose with mineral NPK salts was used to determine both the growth rate and the parameters of Michaelis-Menten kinetics (Blagodatsky et al., 2000). Concentrations of all solutions were adjusted to C:N=10 and N:P:K equal to 10:5:1. Volumes of the added solutions were calculated to adjust the soil water content in the samples to 80% of water holding capacity.

All equations were fitted using nonlinear least-squares regression by Marquardt algorithm. Since the difference between two incubation temperatures was equal to 10°C, Q_{10} s were calculated as the ratio between the parameter values at 22°C and 12°C.

The amount of CO_2 increase in the incubation flasks was measured by gas chromatography. Concentration of CO_2 in the headspace gas probes was analysed on Chrom-5 gas chromatograph on 2.5 m column with Porapack-Q using TCD. Carbon

and nitrogen content in soil was measured by CHN-analyser (C. Erba, Italy). All results were obtained in 3–4 replicates and are expressed on an oven-dry weight basis.

3 Results and discussion

3.1 Parameters of microbial growth and substrate utilization

Parameters of glucose utilization were calculated by the modified Michaelis-Menten equation Eq. (4) with a good fit between measured and simulated data (Fig. 1). These parameters were time-, site- and temperature-dependent (Table 1).

Microbial growth on glucose excess was simulated by Eq. (3) (Fig. 2). Maximal specific growth rate (μ_{max}) obtained at the exponential phase of microbial growth was much higher at 22°C than at 12°C with Q_{10} values greater than 2 (Table 1). On the contrary, the values of V_{max} fitted at the lag phase showed temperature acclimation: the ratios of V_{max} at 22°C and 12°C were 1.7 and 1.5 for the forest and arable soils respectively. These Q_{10}s of V_{max} are lower than the value of 2 assigned by Davidson et al., 2006.

The values of K_s, S_n, V_{max}, and μ_{max} reflect the relative abundance of copiotrophic and oligotrophic components of microbial community in soil. Copiotrophic microorganisms grow best at high carbon concentrations, they have a relatively high half-saturation constant and high maximal growth rate. Oligotrophic microorganisms grow best at low carbon concentrations and have a low half-saturation constant and low maximal growth rate (Semenov, 1991). This physiological distinction between the trophic groups is to some extent analogous to the ecological subdivision into *r* and *K* strategists. Microbial growth in soil is usually substrate limited, and the majority of soil microorganisms growing on flushes of substrate caused by seasonal litter fall, rhizodeposition or drying-rewetting events are usually *r* selected. The increased competitiveness due to the adaptation to the substrate depletion conditions is the feature of *K* strategists (Paul and Clark, 1996). Comparative analysis of K_s, S_n, V_{max} and μ_{max} values indicates the

predominant strategy in r-K continuum.

The decline of V_{max}, K_s and S_n associated with SOM depletion and temperature decrease (Table 1) evidence the shift from *r* to *K* selection or to oligotrophy in unfavorable environments. Hence, the oligotrophy increased in the following order: forest soil at 22°C< forest soil at 12°C< arable soil at 22°C< arable soil at 12°C. Less significant parameter changes were observed during the 2 mo incubation. The incubation resulted in the decrease of a readily decomposable native substrate (S_n) in the forest soil, while in the arable soil all the parameters were unchanged.

The changes in glucose utilization parameters with temperature confirm the importance of the canceling effect suggested by Davidson et al. (2006). Both V_{max} and K_s were higher at 22°C than at 12°C in the forest and arable soil (Table 1) canceling the increase of each other. The canceling effect is significant when substrate concentration is close to K_s. In our study S_n was much lower than K_s in both soils. The values of S_n for arable soils obtained by Sikora and McCoy (1990) and Badalucco and Hopkins (1997) in short term incubations were equal to K_s, supporting the hypothesis of the canceling effect in arable soils.

We determined the parameters of the modified Michaelis-Menten equation Eq. (4) at the start of the experiment and after 2 mo incubation (Table 1). S_n value in forest soil at the beginning of the incubation was two times greater, i.e. closer to the K_s value than that after 2 mo incubation. In the field conditions the canceling effect appears to be more significant than in the incubation experiments. Seasonal litter fall, root exudation and turnover, drying-rewetting events considered usually as confounding factors (Kirschbaum, 2006; Reichstein et al., 2005b) can substantially increase S_n values up to the range of K_s values and stimulate temperature acclimation.

If substrate concentration is much higher or significantly lower than K_s, the half-saturation constant becomes insignificant factor for the apparent acclimation, and temperature response depends on Q_{10} s of V_{max} and S_n. At high substrate content not limiting microbial respiration, the whole microbial community exhibited acclimation, while its growing component showed higher temperature sensitivity. Q_{10} s of μ_{max} describing

growing microbial biomass were higher than temperature coefficients of V_{max} reflecting respiratory response of the whole microbial community (Table 1). The fact that microbial growth is more temperature sensitive than maintenance was confirmed by the response of soil microorganisms to extra low temperatures (Panikov et al., 2006). No microbial growth was found at temperatures below 0°C, while maintenance respiration was detected at the temperature as low as –39°C.

Microbial biomass partitioning on growing and sustaining (active, but not growing) components (Blagodatsky and Heinemeyer, 2000) showed that growing component amounts to 10–20% of total biomass only, but the shifts from growing to sustaining physiological state can also contribute to temperature sensitivity changes of soil respiration. Thus, in an experiment with a long-term soil incubation with added labeled glucose (Nicolardot et al., 1994), temperature sensitivity correlated with the glucose decomposition rate: the highest temperature sensitivity was observed at the first stages of the experiment when glucose decomposition rate was the highest. After the added glucose was depleted, and proportion of sustaining biomass increased, the temperature sensitivity decreased significantly.

The highest temperature response of soil respiration without acclimation was detected in the arable and in the forest soils at a low substrate concentration when S_n was lower than K_s. Q_{10} s of S_n (Table 1) were consistent with Q_{10} s of respiration rates at zero concentration of glucose added (Fig. 1).

The changes of the glucose utilization parameters associated with temperature alterations can reflect real physiological temperature adaptation of soil microorganisms as well as the apparent acclimation caused by substrate concentration and quality changes. It is often impossible to differentiate real and apparent acclimation since substrate availability changes along with temperature (Kirschbaum, 2006). Since the S_n values determined in our experiment were also changing with temperature, we also could not differentiate the real and apparent acclimation (Table 1). The interaction between temperature response of soil respiration and substrate availability is eliminated when substrate content is not limiting and microbial respiration is close to V_{max}. Q_{10} s of

V_{max} were lower than 2 (Table 1) assuming the real acclimation of soil microorganisms by glucose excess. Growth and maintenance of soil microorganisms under field conditions are substrate limited, and the significance of real acclimation is still uncertain.

3.2 Temperature response of labile and recalcitrant SOM

Cumulative soil respiration during annual incubation fitted well to the double exponential decay function Eq. (2); R^2=0.99. Soil respiration, rate constants and the size of labile pool were higher in the forest soil reflecting depletion of total and labile SOM in the arable land (Table 2). All the fitted parameters were significantly related to the temperature. The rate constants k_2 were much more sensitive to the temperature than k_1 for both soils. These results confirm the hypothesis that low-quality substrates (i.e. substrates with low proportion of readily decomposable C substances) are mineralized with a higher Q_{10} than labile substrates (Bosatta and Agren, 1999; Knorr et al., 2005; Leifeld and Fuhrer, 2005; Fierer et al., 2006). However, a number of studies reported that the temperature response may not correlate (Dioumaeva et al., 2003; Fang et al., 2005; Reichstein et al., 2005a; Conen et al., 2006) or correlate positively (Liski, 1999; Giardina and Ryan, 2000; Mellilo et al., 2002) with SOM quality. The majority of methodological approaches, including our long-term incubation, estimate the response of two small SOM pools with mean residence time of years and decades. Both pools can be considered labile compared to the old SOM pool, which turns over for centuries and millennia. The sensitivity of this old stable SOM to soil warming is not yet experimentally tested, and is still unknown.

Temperature elevation increased the rate constants and the size of labile SOM pool as well (Table 2). The size of respirable labile C pool (A_0) was 1.3–3.4 times higher at 22°C than at 12°C. Modeling of fixed labile pool (Parton, 1987; Katterer et al., 1998) simulated at the highest incubation temperature 30–35°C suggested that temperature changes affect rate constant only. However, the assumption of constant pool size may be incorrect (MacDonald et al., 1995; Waldrop and Firestone, 2004). The enlargement of the labile pool at higher temperature indicates an increase in the enzymatic

activity stimulating decomposition of recalcitrant SOM. There are two main groups of extracellular enzymes produced by soil microorganisms decomposing macromolecular SOM: oxidative and hydrolytic enzymes. The first group is involved in the convertion of phenolic polymers into labile compounds while the second is used to decompose cellulose. Enhanced oxidative enzyme activity in response to the elevated temperature was proposed as the mechanism providing greater microbial access to the recalcitrant SOM and, therefore, resulting in an increased labile SOM pool (Waldrop and Firestone, 2004). This mechanism can compensate the labile substrate depletion at elevated temperatures. At high temperature the decrease in respiration rate caused by the depletion of readily available substrate is followed by the increase in the initial rate of SOM decomposition. The same mechanism is proposed for the explanation of the apparent acclimation in experiments with soil warming or long term incubation (Eliasson et al., 2005; Kirschbaum, 2006). However, the increase of both S_n (Table 1) and the labile SOM pool A_0 (Table 2) due to temperature elevation found in our experiments proves that no substrate depletion happened. Conversely, lower substrate content was detected at the lower temperature of 12°C. Compensation of the respired labile SOM occurred in both soils studied, with more prominent increase of A_0 in arable soil (Table 2). Thus, our data suggest the importance of a feedback between substrate depletion and microbial access to recalcitrant SOM.

Both methodological approaches used in our experiments gave similar indices of labile C: S_n determined by modified Michaelis-Menten equation is consistent with A_0 simulated by double exponential decay model. Higher S_n values at 22°C correspond well to the increased labile pool A_0 at this temperature (Tables 1 and 2) compared to 12°C. Parameters of Michaelis-Menten equation are more informative for understanding apparent acclimation and variability of temperature sensitivity as a function of high quality substrate concentration. As mentioned, canceling effect is significant when the concentration of readily decomposable substrate is comparable to the K_s concentration by degradation of the most labile SOM fractions. When the pool of recalcitrant and stable SOM is being decomposed, the level of S_n is lower than K_s, and the canceling

effect is of minor importance.

This study is the starting point to assess biologically and ecologically meaningful parameters V_{max}, K_s, S_n, which are necessary to determine respiration response to changing temperature. Since we can not derive these parameters from individual studies on SOM decomposition, the determination of these parameters at the early and advanced stages of decomposition over the whole range of temperatures in a wide variety of soils would be useful for modeling temperature sensitivity of SOM decomposition.

4 Conclusions

Our data suggest that the parameters of microbial growth and substrate utilization are useful for explanation of dependence of temperature sensitivity of soil respiration on the concentration of readily decomposable substrate. Temperature response of SOM decomposition is the highest when the substrate concentration is very low ($S+S_n \ll K_s$). The canceling effect of V_{max} and K_s temperature sensitivities is negligible, and acclimation does not take place. As substrate content increases to the K_s values ($S+S_n \cong K_s$), the canceling effect is of great importance as a main mechanism of acclimation, i.e. substantial lowering of the temperature sensitivity of microbial respiration. When the substrate concentration does not limit microbial respiration ($S+S_n \gg K_s$), soil CO_2 efflux is close to V_{max}, and the canceling effect has minor importance. The acclimation depends on the portion of growing microbial biomass in total microbial C pool: the larger growing biomass pool is, the higher temperature sensitivity of microbial respiration is detected. We suggest that the canceling effect is more important in the field experiments than in laboratory incubations since the concentration of readily decomposable substrate under field conditions is often higher due to litter fall, drying-rewetting events, translocation of rhizodeposits into the soil etc. It means that temperature sensitivity of soil respiration depends on the concentration of decomposable substrate regardless of its origin. Hence, the approach used in this work improves our understanding of the

effect of confounding factors controlling the response of CO_2 efflux to soil warming.

Acknowledgements. This research was supported by the Russian Foundation for Basic Researches (projects 05-04-48441, 06-04-48756, 06-04-90610), Program "Russian Scientific Schools" (grant NS 3096.2006.4) and the Russian Academy of Sciences (program 16).

References

Badalucco, L. and Hopkins, D. W.: Available carbon in soil determined from substrate utilization kinetics: comparison of substrates and soil amendments, J. Microbiol. Methods, 30, 43–47, 1997.

Blagodatsky, S. A., Blagodatskaya, E. V., and Rozanova, L. N.: Kinetics and strategy of microbial growth in Chernozemic soil affected by different long-term fertilization, Microbiology, 63, 298–307, 1994.

Blagodatsky, S. A., Heinemeyer, O., and Richter, J.: Estimating the active and total soil microbial biomass by kinetic respiration analysis, Biol. Fertil. Soils, 32, 73–81, 2000.

Bosatta, E. and Agren, G. I.: Soil organic matter quality interpreted thermodynamically, Soil Biol. Biochem., 31, 1889–1891, 1999.

Bradley, R. L. and Fyles, J. W.: A kinetic parameters describing soil available carbon and its relationship to rate increase in C mineralization, Soil Biol. Biochem., 27, 167–172, 1995.

Conen, F., Leifeld, J., Seth, B., and Alewell, C.: Warming mineralises young and old soil carbon equally, Biogeosciences, 3, 515–519, 2006, http://www.biogeosciences.net/3/515/2006/.

Davidson, E. A., Janssens, I. A., and Luo, Y.: On the variability of respiration in terrestrial ecosystems: moving beyond Q_{10}, Global Change Biol., 12, 154–164, 2006.

Dioumaeva, I., Trumbore, S., Schnur, E. A. G., Goulden, M. L., Litvak, M., and Hirsch, A. I.: Decomposition of peat from upland boreal forest: Temperature dependence and sources of respired carbon, J. Geophys. Res., 108(D3), 8222, doi:10.1029/2001JD000848, 2003.

Eliasson, P. E., McMutrtrie, R. E., Pepper, D. A., Stromgren, M., Linder, S., and Agren, G. I.: The response of heterotrophic CO_2 flux to soil warming, Global Change Biol., 11, 167–181, 2005.

Fang, C., Smith, P., Moncrieff, J., and Smith, J. U.: Similar response of labile and resistant soil organic matter pools to changes in temperature, Nature, 433, 57–59, 2005.

Fierer, N., Colman, B. P., Schimel, J., and Jackson, R. B.: Predicting the temperature dependence of microbial respiration in soil: A continental scale analysis, Global Biogeochem. Cycles, 20, GB3026, doi:10.1029/2005GB002644, 2006.
Giardina, C. P. and Ryan, M. G.: Evidence that decomposition rates of organic carbon in mineral soil do not vary with temperature, Nature, 404, 858–861, 2000.
Ise, T. and Moorcroft, P. R.: The global-scale temperature and moisture dependencies of soil organic carbon decomposition: an analysis using a mechanistic decomposition model, Biogeochemistry, 80, 217–231, 2006.
Jarvis, P. and Linder, S.: Constraints to growth of boreal forests, Nature, 405, 904–905, 2000.
Katterer, T., Reichstein, M., Andren, O., and Lomander, A.: Temperature dependence of organic matter decomposition: a critical rewiev using literature data analysed with different models, Biol. Fertil. Soils, 27, 258–262, 1998.
Kirschbaum, M. U. F.: The temperature dependence of organic matter decomposition – still a topic of debate, Soil Biol. Biochem., 38, 2510–2518, 2006.
Knorr, W., Prentice, I. C., House, J. I., and Holland, E. A.: Long-term sensitivity of soil carbon turnover to warming, Nature, 433, 298–301, 2005.
Leifeld, J. and Fuhrer, J.: The temperature response of CO_2 production from bulk soils and soil fractions is related to soil organic matter quality, Biogeochemistry, 75, 433–453, 2005.
Liski, J., Ilvesniemi, H., Makela, A., and Wiestman, K. J.: CO_2 emissions from soil in response to climatic warming are overestimated – the decomposition of old soil organic matter is tolerant to temperature, Ambio, 28, 171–174, 1999.
MacDonald, N. W., Zak, D. R., and Pregitzer, K. S.: Temperature effect on kinetics of microbial respiration and net nitrogen and sulfur mineralization, Soil Sci. Soc. Amer. J., 59, 233–240, 1995.
Melillo, J. M., Steudler, P. A., Aber J. D., Newkirk, K., Lux, H., Bowles, F. P., Catricala, C., Magill, A., Ahrens, T., and Morrisseau, S.: Soil warming and carbon cycle feedbacks to the climate system, Science, 298, 2173–2176, 2002.
Nicolardot, B., Fauvet, G., and Chenby, D.: Carbon and nitrogen cycling through soil microbial biomass at various temperatures, Soil Biol. Biochem., 26, 253–261, 1994.
Panikov, N. S., Blagodatsky, S. A., and Glagolev, M. V.: Determination of microbial mineralization activity in soil by modified Wright and Hobbie method, Biol. Fertil. Soils, 14, 280–287, 1992.
Panikov, N. S., Flanagan, P. W., Oechel, W. C., Mastepanov, M. A., and Christensen, T. R.:

Microbial activity in soils frozen to below –39°C, Soil Biol. Biochem., 38, 785–794, 2006.
Panikov, N. S. and Sizova, M. V.: A kinetic method for estimating the biomass of microbial functional groups in soil, J. Microbiol. Methods, 24, 219–230, 1996.
Parton, W. J., Schimel, D. S., Cole, C. V., and Ojima, D. S.: Analysis of factors controlling soil organic matter levels in Great Plains grasslands, Soil Sci. Society Amer. J., 51, 1173–1179, 1987.
Paul, E. A. and Clark, F. E.: Soil Microbiology and Biochemistry, 2nd ed., Academic Press, San Diego, 1996.
Reichstein, M., Katterer, T., Andren, O., Ciais, P., Schulze, E.-D., Cramer, W., Papale, D., and Valentini, R.: Temperature sensitivity of decomposition in relation to soil organic matter pools: critique and outlook, Biogeosciences, 2, 317–321, 2005, http://www.biogeosciences.net/2/317/2005/.
Reichstein, M., Subke, J.-A., Angeli, A., and Tenhunen, J. D.: Does the temperature sensitivity of decomposition of soil organic matter depend on water content, soil horizon, or incubation time?, Global Change Biol., 11, 1754–1767, 2005b.
Semenov, A. M.: Physiological bases of oligotrophy of microorganisms and concept of microbial community, Microb. Ecol., 22, 239–247, 1991.
Sikora, L. J. and McCoy, J. L.: Attempts to determine available carbon in soils, Biol. Fertil. Soils, 9, 19–24, 1990.
Thornley, J. H. M. and Cannell, M. G. R.: Soil carbon storage response to temperature: an hypothesis, Annals Botany, 87, 591–598, 2001.
Waldrop, M. P. and Firestone, M. K.: Altered utilization patterns of young and old soil C by microorganisms caused by temperature shifts and N additions, Biogeochemistry, 67, 235–248, 2004.

Table 1. Parameter values of substrate utilization kinetics after glucose addition to the soil before and after 2 mo incubation. Values in parenthesis indicate the error of parameter.

	Initial sample	Sample after incubation			Initial sample	Sample after incubation		
Temperature °C	22	22	12	Q_{10}	22	22	12	Q_{10}
		forest soil				arable soil		
V_{max},μg C-CO_2g^{-1}h^{-1}	15.6 (0.5)	15.1 (0.4)	9.1 (0.3)	1.7	2.9 (0.3)	2.4 (0.2)	1.6 (0.1)	1.5
K_s, μg Cg^{-1}	50.6 (6.8)	43.0 (5.2)	33.3 (3.8)	1.3	12.2 (1.3)	18.0 (2.7)	11.4 (1.6)	1.6
S_n, μgC g^{-1}	10.8 (2.4)	5.2 (1.1)	2.2 (0.8)	2.4	1.8 (0.8)	2.7 (0.8)	1.1 (0.3)	2.4
μ_{max}, h^{-1}	nd	0.29 (0.02)	0.14 (0.01)	2.1	nd	0.14 (0.01)	0.07 (0.004)	2.0

Table 2. Parameter values of microbial respiration by the decomposition of soil oragnic matter (k_1 and k_2 rate constants of labile and recalcitrant pools, $A_\circ$ – pool size of labile substrate). Values in parenthesis indicate the error of the parameter.

Temperature ˚C	12	22	Q_{10}	12	22	Q_{10}
		forest soil			arable soil	
$A_\circ$ ($\times 10^{-2}$)	2.1 (0.03)	3.1 (0.12)	1.5	0.64 (0.08)	2.2 (0.10)	3.4
k_1, days^{-1} ($\times 10^{-2}$)	2.1 (0.07)	1.8 (0.15)	0.9	1.6 (0.27)	2.1 (0.24)	1.3
k_2, days $^{-1}$ ($\times 10^{-4}$)	0.62 (0.01)	1.4 (0.05)	2.3	0.72 (0.03)	1.9 (0.04)	2.6

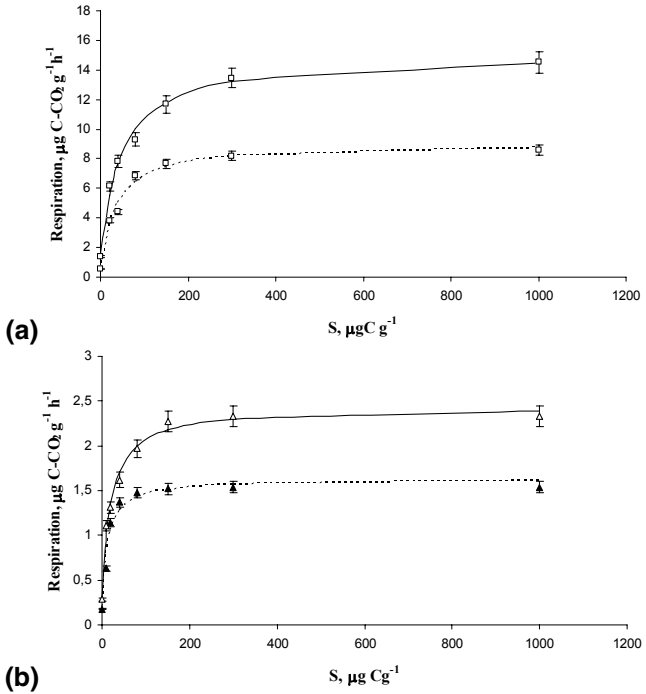

Fig. 1. Forest **(a)** and arable **(b)** soil respiration response to increasing concentration of added glucose determined at 22°C (solid line) and 12°C (dashed line) approximated by Eq. (2) (R^2=0.95–0.99). Error bars indicate standard deviations, n=5.

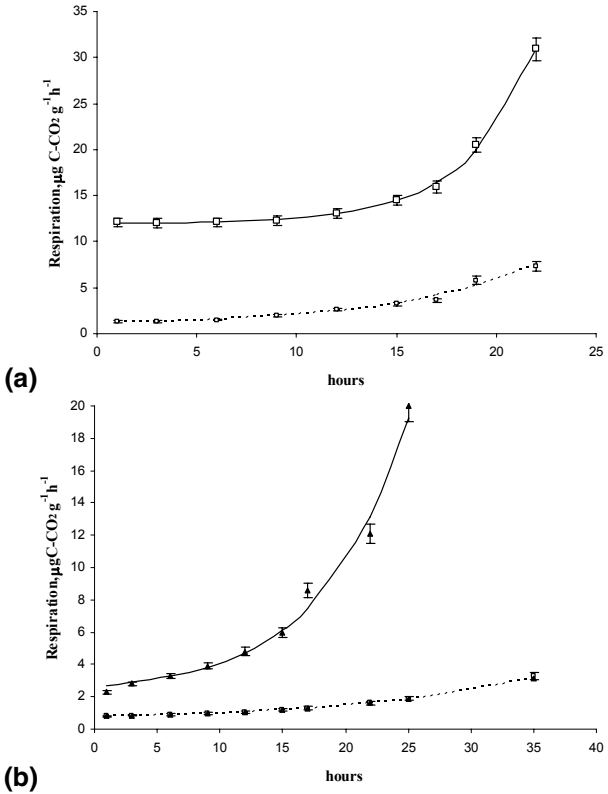

Fig. 2. Dynamics of forest **(a)** and arable **(b)** soil respiration amended with glucose excess (4 mgCg-1 soil) in response to incubation temperature: 22°C (solid line) and 12°C (dashed line) simulated by Eq. (3) (R^2=0.93–0.98). Error bars indicate standard deviations, n=5.